A Comparison of Bird Digestive Systems by Diet

Research Thesis

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by

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Abstract

The vertebrate digestive system can be modified to accommodate a diversity of diets. In general, herbivores tend to have longer, more complex digestive systems while carnivores have smaller, less elaborate digestive systems, but most of the research in this area examines mammalian morphology. Accordingly, the goal of this study was to determine the influence of diet on digestive system morphology in birds. I expected the size of the intestines, cecum (if present), proventriculus, and gizzard to be larger in herbivorous birds and smaller in carnivorous birds. Birds of varying diets were dissected and their digestive systems (intestines, cecum, proventriculus, and gizzard) were weighed. Additionally, each organ's percent contribution to total body weight was calculated. Diet was determined by literature and by the gizzard contents of each bird. A mixed model was used for comparisons with the percentage of body mass due to organ weight as the dependent variable, bird diet as a fixed effect, and family as a random effect. Results from 34 birds revealed that diet affected size of the proventriculus but not the size of the intestines, gizzard, cecum, or the total digestive system. The proventriculus size was largest in insectivores and smallest in herbivores, with omnivores having an intermediately-sized proventriculus. Contrary to previous studies, our study did not support the hypothesis that herbivorous diets lead to a larger, more elaborate digestive system than carnivorous diets in birds. Previous studies either focused on one specific species or examined a much wider variety of species. Because some feeding strategies in our study were limited to only a single taxon, our ability to differentiate between taxonomical differences and trophic differences was hindered.

Introduction

Mammals have extremely diverse digestive systems. Herbivorous mammals tend to have longer, more complex digestive systems while carnivorous mammals have smaller, less elaborate digestive systems (DeGolier et al. 1999). This may be because herbivorous mammals need more time and energy to break down plant cellulose (DeGolier et al. 1999). Ruminants, for example, have large stomachs that are divided into multiple compartments in order to digest roughages such as straw and hay (Hogan and Phillips 2008). On the other hand, the monogastric digestive system has a smaller, simple stomach for highly digestible concentrates often found in meat protein and certain plants (Tsukahara and Ushida 2000). Comparatively, the avian digestive system is distinct from ruminant, monogastric, or all other mammalian digestive systems.

The distinctiveness in birds is a direct result of their evolutionary history. Birds differentiated from their reptilian ancestors during the early Triassic period, or millions of years after mammals had already diverged from reptiles (Ostrom 1975). This means that birds share very few derived characteristics with mammals. Since mammals and birds evolved independently, they have very different intestinal morphology. For example, whereas mammals evolved teeth to physically break down food, birds swallow chunks of food whole and use three vital digestive organs to breakdown food. Initially, many birds utilize a crop that allow birds to temporarily store large amounts of food and then fly to a safer position to begin digestion. Secondly, the proventriculus breaks down the food with strong stomach acids. Lastly, the gizzard is used to mechanically grind large chunks of food (Turk 1982). Only a few studies have examined the variability of the avian digestive system among different species.

Similar to mammals, birds exhibit variation in gut size and complexity. Diet generally dictates the overall development of avian digestive system morphology (Karasov et al. 2011). Since bird diets vary greatly, their respective digestive systems also demonstrate a degree of variance. Granivorous birds (seed-eaters) tend to have larger gizzards than their frugivorous (fruit-eaters) counterparts in order to grind the harder seeds (Gionfriddo and Best 1996, Krautwald-Junghanns et al. 2002). In addition, very few diets are restricted to one food group; diet often changes based on availability and season (DeGolier et al. 1999).

The goal of this study was to determine the influence of various bird diets on the digestive system morphology. I expected the size of the intestines, cecum (if present), proventriculus, and gizzard will be larger in herbivorous birds and smaller in carnivorous birds. This project contributes to the growing knowledge of the form and function of bird digestive morphology.

Methods

Research was conducted in Lima, Ohio between May and August 2016. The birds used were previously salvaged and donated to The Ohio State's University's Museum of Biological Diversity. Total mass of the birds was recorded to the nearest 0.001 g. Larger birds were weighed on a top loading balance to the nearest 0.1 g. The body cavity containing the digestive system was extracted. The intestines, cecum (if present), proventriculus, and gizzard were weighed to the nearest 0.001 g. The gizzard was emptied, rinsed with water, and patted dry before being weighed.

Diets were assigned to one of the following categories: carnivore (eating either terrestrial or aquatic vertebrates), herbivore, omnivore, or insectivore. Diet was determined using two methods: 1. Based on a literature search using Poole (2016), 2. Based on gizzard contents.

The total digestive system was calculated by the sum of the intestines, proventriculus, gizzard, and cecum. The percentage of each organ, relative to total bird mass, was calculated. Data from two birds of the same species were averaged together to prevent pseudoreplication. A mixed model was used for comparisons with the percentage of body mass due to organ weight as the dependent variable, bird diet as a fixed effect, and family as a random effect. All analyses were conducted in JMP (version 11.0.0, SAS Institute Inc. 2013).

Results

A total 39 birds were examined. According to the literature, 12 herbivores, 17 omnivores, 7 insectivores, and 3 carnivores were examined (Table 1). According to the gizzard contents of each bird, 16 herbivores, 4 omnivores, 11 insectivores, and 1 carnivore were examined (7 gizzards were found empty; Table 1). Only 34 species were included in the analyses because carnivores were excluded due to low sample sizes, and individuals of the same species were averaged together. The average mass was 131.4±224.9 g (range 9.7-1113.9 g, N=37). The intestines and the gizzard comprised the majority of the total digestive system weight (Table 2). The size of the total digestive system was highly correlated with the mass of the bird ($r^2 = 0.71$; $F = 90.38$, $N = 39$, $P<0.0001$; Figure 1).

Diet, as determined from the literature, affected size of the proventriculus (F=6.38, N=33, P=0.0057; Figure 2A) but not the size of the intestines (F=0.39, N=31, P= 0.68), gizzard (F=0.11, N=33, P=0.89), cecum (F=1.36, N=10, P=0.33), or the total digestive system (F=0.55, N=33, P=0.59). The diet, as determined by gizzard contents, revealed analogous results: proventriculus varied with diet (F=4.06, N=29, P=0.031; Figure 2B), but intestines (F=0.34, N=27, P=0.72), gizzard (F=0.28, N=29, P=0.76), cecum (F=0.48, N=11, P=0.51), and total digestive system (F=0.13, N=29, P=0.88) did not. Insectivores had a larger proventriculus than herbivores or omnivores when using either diet determination method (Figure 2).

Discussion

The results revealed a correlation between proventriculus size and diet. The proventriculus uses digestive enzymes to initially break down food before it enters the gizzard. In the birds examined, the proventriculus tends to be larger in insectivores than in any other diet type. The insectivorous birds may potentially have a more developed proventriculus because they need more digestive enzymes to break down coarse insects. This correlates with studies that show that finer food particles can negatively affect the development of the proventriculus whereas coarse particles result in a well-developed proventriculus (Al-Masri 2006, Zaefarian et al. 2016).

Although there was a correlation between diet and proventriculus size, the size of the other digestive organs and the total digestive system did not vary with diet. Other studies, however, did show clear modifications in digestive morphology with respect to diet. For example, as the proportion of seeds and plants increase in the diet, the size of the gizzard increased for both individual species (Davidson and Scott 1988) and among species (Barnes and

Thomas 1987). Overall, the herbivorous species had consistently heavier gizzards and ceca than their carnivorous or omnivorous counterparts (DeGolier et al. 1999). Our study did not demonstrate similar results because other studies had significantly reduced taxonomic variability. For example, while our study had 7 herbivorous species, there were only 12 herbivorous specimens to represent this many species. Comparatively, Barnes and Thomas (1987) had only three herbivorous species yet 49 specimens to represent those species. In a similar study by Kehoe and Ankney (1985), only five species of ducks were studied yet they found that differences in digestive morphology was due to diet using a staggering total of 365 specimens. In this study and others like it, the number of species is not as important as the number of individuals representing those species in each diet category. This is because an increased number of specimens per species minimizes other confounding factors including diet or health at the time of death, ecosystem variation in climate and food availability, and individual variation in morphology (Miller 1975, Ricklefs and Travis 1980, Paulus 1982, Whyte and Bolen 1985).

In addition to individual and taxonomic variability, a series of other factors including season, community composition, and prey availability can affect digestive morphology. While our study did not take a proportional number of birds from each season, other studies indicate that birds demonstrate a slight increase in gut size in the autumn and early winter seasons (Paulus 1982, Whyte and Bolen 1985). Furthermore, studies show that avian community organization has an impact on gut morphology as well. Ricklefs and Travis (1980) claim that a large-scale avian community might have a negative impact on gut size, even within species, when compared with smaller communities. Since these factors contribute to digestive morphology, it is important to look at experimental studies wherein these extraneous variables are controlled. For instance, a study that fed turkey, corn, or alfalfa to mallards in a controlled environment found a strong correlation between heavier digestive organs in herbivorous mallards compared to carnivorous ones (Miller 1975). Future studies should control or measure these extraneous variables when examining how diet influences digestive morphology.

Because the results derived from literature corresponded with the results derived from gizzard contents, our method of diet determination had no overall bearing on the conclusion. Additionally, other studies that used primarily diet by literature (Zaefarian et al. 2016) came to the same conclusion with studies that primarily relied on diet by gizzard contents (DeGolier et al. 1999). The choice of method, however, depends on the level of detail researchers need about the diet of the bird (Table 3). Diet by literature is most beneficial for researchers seeking general information about a broad group or species. For example, a study about antioxidant levels in birds included general diet information as determined by literature (Cohen et al. 2009). Diet determination by gizzard content is preferential for studies that measure specific changes between individual birds or in one species at different times of the year. In a study of aerial insectivores in South Africa, bird stomachs were collected, dissected, and sorted by content to compare the diets in sixteen passerine species (Kopij 2000). In another study of bird diets in Northeastern Venezuela, researchers used a third technique. Tartaric emetic was administered to force birds to regurgitate food in their crop to compare diet with previous literature (Poulin et al. 1994). In a similar study in North Carolina, researchers used a crop flushing technique to refine and specify which exact insects were eaten by the insectivorous bird population (Moorman et al. 2007). However, this method of diet determination may increase the risk of mortality (Durães and Marini 2003). Another fourth method used to assign diet categories is examining the turnover rate of carbon-13 in the tissues of birds (Hobson and Clark 1992). The method of diet determination depends on the depth of information required by the researcher and logistical constraints (Table 3). However, we recommend that different diet determination methods not be used in conjunction in the same study (i.e. – using gizzard contents, unless the gizzard is empty and then switching to literature for a subset of individuals), unless the purpose of that study is to compare diet determination methods as ours did.

Besides using a consistent method for determining diet for every individual in the study, we also recommend the following refinements for future studies. Unfortunately, we had too few carnivores represented in our data set to warrant their inclusion in the final analyses. Reducing taxonomic variability and while still expanding the number of individuals representing each taxa could further elucidate the relationship between diet and morphology in future studies. In addition, future studies should consider how season, community, and prey availability affects the relationship between diet and digestive morphology.

Literature Cited

Al-Masri, M. R. (2006). "Productive performance and digestive tract size of broiler chicks fed a conventional or an all vegetable ingredients diet". *Journal of Applied Animal Research* 30 (1): 81-84.

Barnes, Gregory G. and Vernon G. Thomas (1987). “Digestive organ morphology, diet, and guild structure of North American Anatidae”. *Canadian Journal of Zoology* 65 (7): 1812-1817.

Cohen, Alan A., Kevin J. McGraw, and W. Douglas Robinson (2009). “Serum antioxidant levels in wild birds vary in relation to diet, season, life history strategy, and species”. *Oecologia* 161 (4): 673-683.

Davidson, Ankney C. and David M. Scott (1988). “Size of digestive organs in breeding Brown-headed Cowbirds, *Molothrus ater*, relative to diet”. *Canadian Journal of Zoology* 66 (6): 1254-1257.

DeGolier, Teresa F., Sheila A. Mahoney, and Gary E. Duke (1999). "Relationships of avian cecal lengths to food habits, taxonomic position, and intestinal lengths". *The Condor* 101 (3): 622-634.

Durães, Renata and Miguel Ângelo Marini. (2003). “An evaluation of the use of tartar emetic in the study of bird diets in the Atlantic Forest of southeastern Brazil”. *Journal of Field Ornithology* 74 (3): 270-280.

Gionfriddo, James P. and Louis B. Best (1996). "Grit-use patterns in North American birds: the influence of diet, body size, and gender". *The Wilson Bulletin* 108 (4): 685-696.

Hobson, K. and R. Clark (1992). “Assessing avian diets using stable isotopes I: turnover of 13c in tissues”. *The Condor* 94(1), 181-188.

Hogan, J. P. and C. J. C. Phillips (2008). "Nutrition and the welfare of ruminants". ARBS *Annual Review of Biomedical Sciences* 10: T33-T50.

Karasov, William H., Carlos M. del Rio, and Enrique Caviedes-Vidal (2011). "Ecological physiology of diet and digestive systems". *Annual Review of Physiology* 106 (4): 675-686.

Kehoe, F. and Davidson C. Ankney (1985). "Variation in digestive organ size among five species of diving duck". *Canadian Journal of Zoology* 63 (10): 2339-2342.

Kopij, G. (2000). "Diet of granivorous and frugivorous passerines in South African grassland". *South African Journal of Wildlife Research* 30 (4): 135-138.

Krautwald-Junghanns, Maria-Elisabeth, Anja Stahl, Michael Pees, Frank Enders, and Thomas Bartels (2002). "Sonographic investigations of the gastrointestinal tract of granivorous birds". *Veterinary Radiology & Ultrasound* 43 (6): 576-582.

Miller, Michael R. (1975). "Gut morphology of mammals in relation to diet quality". *The Journal of Wildlife Management* 39 (1): 168-173.

Moorman, Christopher E., Liessa T. Bowen, John C. Kilgo, Clyde E. Sorenson, and James L. Hanula (2007). "Seasonal diets of insectivorous birds using canopy gaps in a bottomland forest". *Journal of Field Ornithology* 78 (1): 11-20.

Ostrom, John H. (1976). "Archaeopteryx and the origin of birds". *Biological Journal of the Linnean Society* 8 (2): 91-182.

Paulus, Stuart L. (1982). "Gut morphology of the gadwalls in Louisiana in winter". *The Journal of Wildlife Management* 4 (2): 483-489.

Poole, A. Ed. (2016). Birds of North America Online. Ithaca: Cornell lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu.proxy.lib.ohio-state.edu/bna/species/.

Poulin, B., G. Lefebvre, and R. McNeil. (1994). “Diets of land birds from Northeastern Venezuela”. *The Condor* 96 (2): 354-367.

Ricklefs, Richard E. and Joseph Travis (1980). “A Morphological Approach to Avian Community Organization”. *The Auk* 97 (2): 321-338.

Tsukahara, Theodore and Kaznuri Ushida (2000). "Effects of animal or plant protein diets on cecal fermentation in guinea pigs (*Cavia porcellus*), rats (*Rattus norvegicus*) and chicks (*Gallus gallus domesticus*)". *Comparative Biochemistry and Physiology. Part A, Molecular & integrative Physiology* 127 (2): 139-146.

Turk, D.E. (1982). "The anatomy of the avian digestive tract as related to feed utilization". *Poultry Science* 61 (7): 1225-1244.

Whyte, Richard J. and Eric G. Bolen (1985). “Variation in mallard digestive organs during winter”. *The Journal of Wildlife Management 49* (4): 1037-1040.

Zaefarian, F., M.R. Abdollahi, and V. Ravindran (2016). “Particle size and feed form in broiler diets: impact on gastrointestinal tract development and gut health”. *World’s Poultry Science Journal* 72 (2): 277–290.

Table 1: Common name, scientific name, family, and diet (both from literature and gizzard content) used in this study. Literature diet was obtained from Poole (2016).

Common Name	Scientific Name	Family	Diet (literature)	Diet (gizzard contents)
American Crow	*Corvus brachyrhynchos*	Corvidae	Omnivore	
American Goldfinch	*Spinus tristis*		Herbivore	Herbivore
American Robin	*Turdus migratorius*	Turdidae	Omnivore	Herbivore
American Robin	*Turdus migratorius*	Turdidae	Omnivore	Omnivore
American Robin	*Turdus migratorius*	Turdidae	Omnivore	Herbivore
Blue Jay	*Cyanocitta cristata*	Corvidae	Omnivore	Herbivore
Blue-headed Vireo	*Vireo solitarius*	Vireonidae	Insectivore	Insectivore
Blue-winged Teal	*Anas discors*	Anatidae	Omnivore	Herbivore
Carolina Chickadee	*Poecile carolinensis*	Paridae	Omnivore	Herbivore
Cedar Waxwing	*Bombycilla cedrorum*	Bombycillidae	Herbivore	
Cliff Swallow	*Petrochelidon pyrrhonota*	Hirundindae	Insectivore	Insectivore
Common Grackle	*Quiscalus quiscula*	Icteridae	Herbivore	Omnivore
Common Grackle	*Quiscalus quiscula*	Icteridae	Herbivore	
Common Grackle	*Quiscalus quiscula*	Icteridae	Herbivore	
Common Nighthawk	*Chordeiles minor*		Insectivore	Insectivore
Cooper's Hawk	*Accipiter cooperii*	Accipitridae	Carnivore	
Dark-eyed Junco	*Junco hyemalis*	Emberizidae	Herbivore	Herbivore
Dark-eyed Junco	*Junco hyemalis*	Emberizidae	Herbivore	
Eastern Kingbird	*Tyrannus tyrannus*	Tyrannidae	Insectivore	Omnivore
European Starling	*Sturnus vulgaris*	Sturnidae	Omnivore	
Grasshopper Sparrow	*Ammodramus savannarum*	Emberizidae	Omnivore	Herbivore

Killdeer	*Charadrius vociferus*	Charadriidae	Insectivore	Insectivore
Lark Sparrow	*Chondestes grammacus*	Emberizidae	Herbivore	Herbivore
Lesser Scaup	*Aythya affinis*	Anatidae	Carnivore (Aquatic Invertebrates)	Herbivore
Mallard	*Anas platyrhynchos*	Anatidae	Omnivore	Herbivore
Northen Flicker	*Colaptes auratus*	Picidae	Omnivore	Herbivore
Northern Cardinal	*Cardinalis cardinalis*	Cardinalidae	Herbivore	Herbivore
Northern Cardinal	*Cardinalis cardinalis*	Cardinalidae	Herbivore	Herbivore
Northern Cardinal	*Cardinalis cardinalis*	Cardinalidae	Herbivore	Insectivore
Northern Flicker	*Colaptes auratus*	Picidae	Omnivore	Insectivore
Red-bellied Woodpecker	*Melanerpes carolinus*	Picidae	Omnivore	Herbivore
Red-bellied Woodpecker	*Melanerpes carolinus*	Picidae	Omnivore	Insectivore
Red-tailed Hawk	*Buteo jamaicensis*	Accipitridae	Carnivore (Terrestrial Vertebrates)	Carnivore (Terrestrial Vertebrates)
Vesper Sparrow	*Pooecetes gramineus*	Emberizidae	Omnivore	Insectivore
Western Kingbird	*Tyrannus verticalis*	Tyrannidae	Insectivore	Insectivore
White Throated Sparrow	*Zonotrichia albicollis*	Emberizidae	Omnivore	Omnivore
White-Breasted Nuthatch	*Sitta carolinensis*	Sittidae	Omnivore	Insectivore
Willow Ptarmigan	*Lagopus lagopus*	Phasianidae	Herbivore	Herbivore
Yellow-billed Cuckoo	*Coccyzus americanus*	Cuculidae	Insectivore	Insectivore

Table 2: Mean, standard deviation, and sample size of various digestive organs and the total digestive system (calculated by the sum of the intestines, proventriculus, gizzard, and cecum).

Organ	Mean	SD	Sample Size
Intestines	0.051	0.016	32
Proventriculus	0.005	0.002	34
Gizzard	0.034	0.011	34
Total Digestive System	9.001	2.155	34

Table 3: Advantages and disadvantages of different methodology for determining diet.

Diet Determination Method	Advantages	Disadvantages
Literature	• Exhaustive information about every bird species provides an accurate representation of general diet composition	• Diet of a single species significantly varies based on seasons, age, and a plethora of other environmental factors • Difficult to assign to one diet category
Gizzard contents	• Most direct representation of the diet • Straightforward designation into a diet category	• Requires dead birds • Information on the bird's diet is limited to the moment that each individual bird dies • Birds of the same species may have a drastically different diet (open to outliers) • Identifying gizzard contents may be difficult • Gizzard may be empty
Crop flushing	• Use of live birds allows direct representation of diet • Able to compare birds of the same species in different habits • Ability to collect raw data at a specific time	• Identifying regurgitated material may be difficult • Crop maybe be empty • Possible detrimental health effects on the birds
Carbon dating	• Able to assign birds to distinct categories based solely on isotopes • As opposed to gizzard contents, only bird muscle tissues are necessary to identify diet	• Not specific enough to identify what exactly was consumed by the bird • Only a comparison of similar isotope levels amongst birds (open to outliers) • Requires dead birds

Figure 1: The mass of the total digestive system increased with the total mass of the bird.

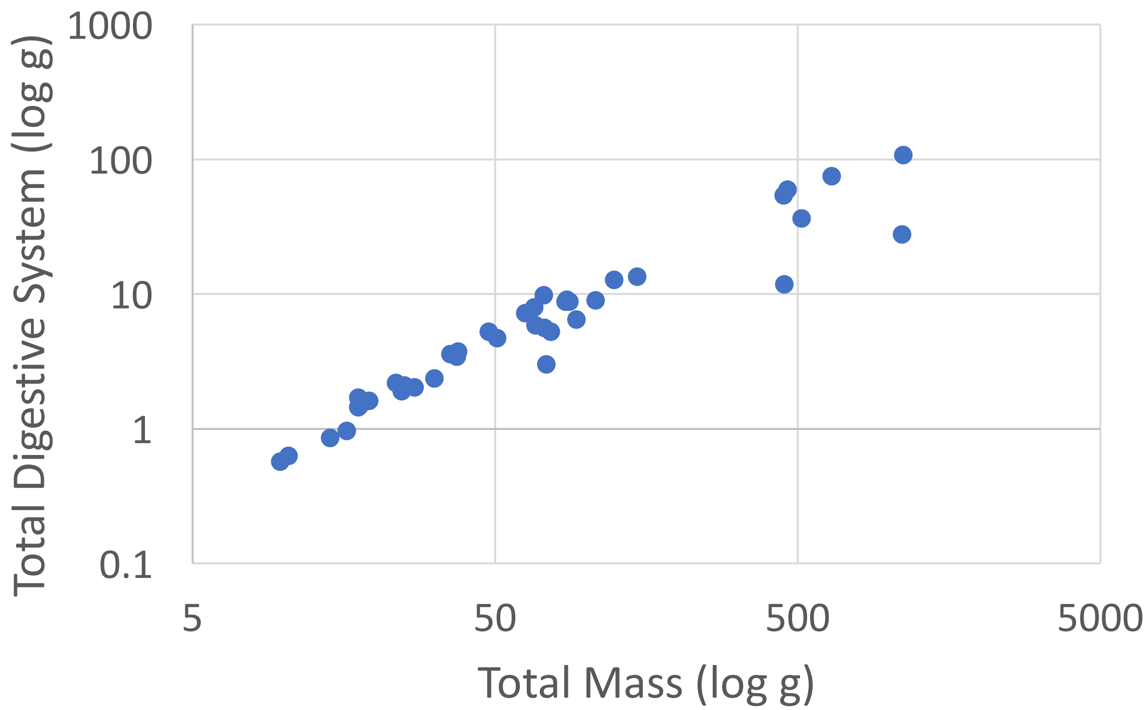

Figure 2: Proventriculus size adjusted for total body weight was largest in insectivores and smallest in herbivores as determined by both A) literature and B) gizzard contents.